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BEHAVIORAL ASPECTS OF RIGHTING IN TWO ASTEROIDS FROM THE PACIFIC COAST OF NORTH AMERICA

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The righting reaction in Asteroids may be defined as the ability of sea stars, when placed on their aboral surface, to turn over onto the normal position with the oral surface down.

Reese (1966) listed four basic questions concerning the righting reaction in asteroids: (1) What is the nature of the stimulus that evokes righting? (2) Is the coordination of the righting movements under central (radial and ring) or peripheral (series of reflexes) control? (3) Is there a pair of arms which tend to initiate and lead in righting, that is, is there a physiological anterior end in righting? (4) What are the sources of variation in righting?

Righting in asteroids was first studied experimentally by Vulpian (1862), Romanes and Ewart (1881), and Romanes (1885), but they were mostly concerned with the nature of the stimulus that evoked righting. Since these early studies, numerous descriptions of the righting behavior of various species of asteroids have appeared.

Detailed descriptions of the righting movements are given by Jennings (1907), Moore (1910a, 1910b, 1939), Cole (1913a), Kjerschow-Agersborg (1918), Russell (1919), Ohshima (1940), and Rodenhouse and Guberlet (1946).

The specific movements in the righting reactions of sea stars show some variability (Jennings, 1907; Ohshima, 1940), but may, in general, be classified into three basic righting methods (Ohshima, 1940). (1) Somersaulting, all five arms bend aborally bringing the tips of each arm in contact with the substratum (dorsal reflex). Typically, two adjacent arms then twist so that their oral surfaces face each other. As these two arms move to the side of the animal (walking distally), the remaining arms rise (orally) and swing over the sea star. In effect, the animal turns a somersault. (2) Folding over, three arms lower aborally. The two outer, non-adjacent, arms that have lowered twist so that their oral surfaces face each other. As these two arms move to the side of the animal, the unattached arms, instead of elevating, fold over the rest of the body. Finally, the middle arm doubles under the animal. (3) Forming the tulip, all five arms rise orally into a "budlike" shape with the aboral surface facing outward. Several arms swing over, causing the center of gravity to be changed, thereby, forcing the animal to turn over onto the normal position.

All the variations seen in asteroid righting are apparently derived from these three basic methods (Reese, 1966).

In addition to describing righting, many of these authors gave considerable attention to the question of arm preference during righting. Jennings (1907), in

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an extensive report on the behavior of *Astrometis sertulifera* (=*Asterias forreri*), found that the pair of arms lying immediately adjacent to the madreporite lead in righting. Similar findings have been reported by Cole (1910, 1913a, 1913b), in *Asterias forbesi*, Kjerschow-Agersborg (1918, 1922) in *Pycnopodia helianthoides*, and Russell (1919), in *Asterias gibbosa*. Cowles (1910, 1911) found that in *Echinaster crassipina*, some individuals showed a tendency to right on a specific pair of arms, which Cowles did not identify. Hamilton (1922a), working with *Pisaster ochraceus*, believed that the arm which "pulled the strongest" became the leading arm in righting. Ohshima (1940) studied righting in *Oreaster nodosus* and concluded that there was no preference for any arms in righting. Rodenhouse and Guberlet (1946) reported that *Pteraster tesselatus* showed a definite tendency to right on two adjacent arms, but that the specific pair of arms depended on individuals, not species. They also found that the leading arms were not related to the position of the madreporite. Finally, Smith (1950), noted that in *Asterias rubens*, arm preference was related to the bilateral symmetry of the larvae, rather than to greater arm length or greater number of podia.

It is clear that the question posed by Reese (1966, page 174), "Does one pair of arms tend to initiate and lead in the righting movements, that is, is there a functional or physiological anterior end involved in righting?" is unsettled. This study was in part designed to investigate this question.

Much of the published work on Echinoderm behavior, especially righting, has been qualitative and no statistical study on the righting behavior of asteroids has been published. The present paper describes and compares the behavioral aspects of righting in two common rocky intertidal Oregon sea stars *Henricia leviuscula* and *Leptasterias aequalis* by quantitative methods. In addition, the significance of righting to the functional nature of the asteroid nervous system is considered.

Materials and Methods

Species studied

The asteroids *Henricia leviuscula* and *Leptasterias aequalis* were selected because they were available in adequate number, are easily maintained in the laboratory and their righting period was relatively brief. In addition, they differ morphologically.

Henricia leviuscula (Stimpson), 1857 (Order Spinulosa, Family Echinasteridae) is found along the Pacific Coast of North America from the Aleutian Islands (55° N) to San Diego, California (32° 45′N) (Feder and Christensen, 1966). This species has five long, slender, tapering arms which are cylindrical and rather rigid and stiff. *H. leviuscula* is found on intertidal rocky substrata encrusted with sponges and bryozoans (Ricketts and Calvin, 1952; Hopkins and Crozier, 1966). The largest *H. leviuscula* collected for this study measured 10.1 cm.

Leptasterias aequalis (Stimpson), 1862 (Order Forcipulata, Family Asteriidae, Subfamily Asteriinae) ranges from British Columbia (50° N) to Santa Catalina Island, California (33° 25′N) (Feder and Christensen, 1966). *L. aequalis*, a six armed sea star, is rather small, usually less than 6.0 cm in diameter. It also lives in the rocky intertidal (Ricketts and Calvin, 1952). The arms in *L. aequalis* are somewhat flattened and because the endoskeleton is less developed are more flexible and softer than those of *Henricia.*

In 1968, in June and July, 108 specimens of *H. leviuscula* and 111 specimens of *L. aequalis* were collected from rocky intertidal beaches at Yaquina Head (44° 40′N, 124° 04′W), Whale Cove (44° 47′N, 124° 04′W), and Boiler Bay (44° 50′N, 124° 04′W). Another group of 90 *H. leviuscula* were collected in May 1969 at the same places for additional studies. All available sizes of both species were collected and used in the righting trials.

The sea stars were maintained at the Oregon State University Marine Science Center in tanks of well-aerated, running sea water. Once daily measurements of the temperature of the sea water running through the holding tanks and the experimental chamber ranged from 9.5–15° C during both the 1968 and 1969 study periods. Animals were acclimated to aquarium conditions for at least 48 hours prior to study. *L. aequalis* was fed twice a week on small specimens of *Littorina.* The unfiltered laboratory sea water was considered to contain adequate organic material to maintain *H. leviuscula,* since this genus uses filter feeding (Anderson, 1960; Rasmussen, 1965).

Methods of observation

Righting behavior was examined by repeating a standard laboratory righting trial with a large number of individuals of each species, and analyzing the observations made by statistical methods.

Each of the arms of the sea stars was identified during the righting trials using the method devised by Jennings (1907) in his study of the righting reaction of *Astrometis sertulifera.* The aboral, acentric madreporite, located between two adjacent arms (Fig. 1), was used as a landmark for designating arms. By locating the madreporite at 6:00, the arms were named clockwise beginning with arm A (Fig. 1).

Righting trials were run in an aquarium with one plate glass and three plywood sides. The bottom area of the aquarium, 61 × 33 cm, was covered with a smooth plexiglass plate.

Attempts were made throughout the study to keep the environment of the observation aquarium constant. The water was 30 cm deep and continually renewed. The glass side of the observation aquarium always faced away from the laboratory window. Light during experiments was from an overhead fluorescent source. Light intensity, determined by a photographic light meter, was found to be nearly equal in all directions. Therefore, light was considered not to be a directional stimulus.

The general procedure for conducting righting trials for both species was as follows: (1) Using the observers bare hand, an individual sea star was selected from the group in the holding tank and placed in the observation aquarium with its oral surface in contact with the plexiglass plate. (2) After a few minutes, the tip of one arm was grasped with the fingers and the sea star inverted under water. (3) The righting reaction was observed from above and from the side of the aquarium and timed. (4) The sea star was transferred to a separate holding tank and not used again that day, except in the time-size studies described separately.

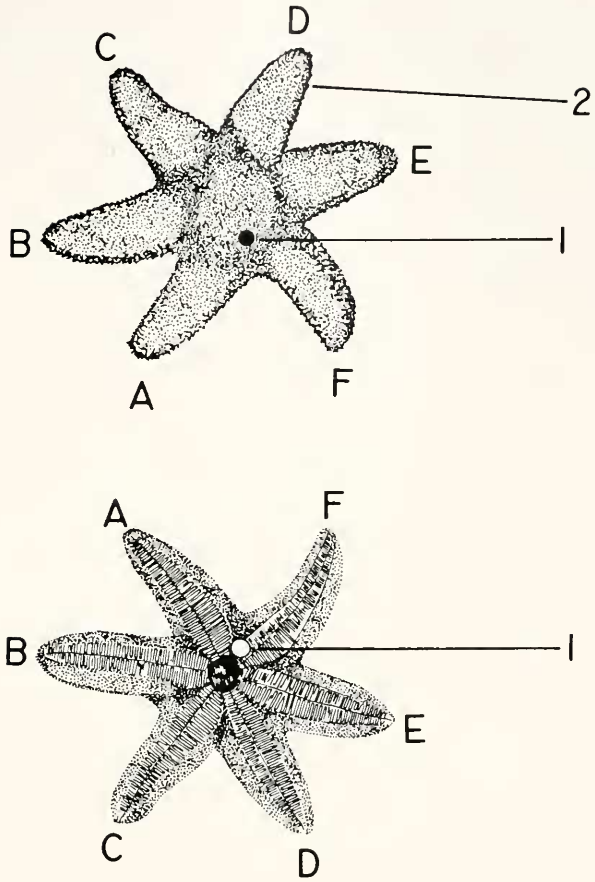

FIGURE 1. Letter designation of arms of *Leptasterias aequalis*; upper diagram, aboral surface, lower diagram, oral surface (ventral), with the position of the madreporite on the aboral surface outlined; 1. madreporite; 2., arm or ray.

Separate trials were not conducted for each of the phenomena being investigated. Instead, during each trial timed observations were made on righting method, pre-righting activity, arm movements and identity of leading arms.

Between July 15 and August 4, 1968, when most of this work was done, 130 trials were conducted using the group of 108 specimens of *H. leviuscula* and 260 trials conducted using the 111 specimens of *L. aequalis* available. During the 1968 trials, the temperature in the observation aquarium was measured intermittently and found to range from 9.5–15° C.

The relationship between righting time and individual size was investigated in both species by additional sets of trials. Approximately ten individuals of each of three size classes were selected for each species. Size classes were based on arm length, or radius (R), measured as the distance from the tip of the arm to the center of the mouth.

Procedures for all time-size trials were as described above, except that each individual was used for three trials, designated A, B and C, with six and 12 hour rest intervals between successive trials. A total of 84 time-size trials were run for each species.

In the case of *L. aequalis* 28 individuals were selected from the 1968 group used in previous trials. Small specimens of *L. aequalis* measured 0.8–1.9 cm, medium, 2.1–2.9 cm, and large, 3.0–4.1 cm. In 1969, 28 specimens of *H. leviuscula* were selected from the 90 individuals available. Small specimens of *H. leviuscula* measured 0.4–2.8 cm, medium, 3.1–4.8 cm, and large, 5.0–10.1 cm.

The data were tested statistically using either the chi-square "goodness-of-fit" test or the Student's "t" test at the 0.05 level of significance.

Results

Righting methods

H. leviuscula used only the somersaulting method to right itself. *L. aequalis* used both the folding over and somersaulting methods when righting. The somersaulting method was used significantly more than folding over ($X^2 = 132$; d.f. = 1; $p = 0.005$). Occasionally *L. aequalis* used a combination of both folding over and somersaulting methods in righting.

Pre-righting period

According to previous studies, when a sea star is first placed on its back, it usually rests on its disc because the aboral surface is convex. It then remains motionless for a variable amount of time before a reaction appears. This is called the latent or quiescent period.

No entirely motionless quiescent period was observed in *H. leviuscula* and *L. aequalis*, neither of which are markedly convex. In both species, some arm and tube foot movements could be detected immediately after inversion. These movements were slight and very difficult to observe, but small, jerking movements by some of the arms were always detected. These slight movements lasted for 0.5 to 3 seconds before major arm movements occurred.

Arm movements

Following the pre-righting period, arm activity increases and leads eventually to resumption of the normal position with the oral surface and tube feet in contact with the substratum. The observations on *H. leviuscula* and *L. aequalis* showed that the chief arm movements used in righting were: (1) Lowering (aboral flexure)—when a sea star was first turned over and placed on its back, the aboral surfaces of the arms were not in contact with the substratum, but slightly elevated above it. The lowering activity permits an arm to come in contact with the substratum. (2) Raising (oral flexure)—raising occurred when an arm rose from the substratum so that it was above the animal with its aboral surface facing away from the mouth and the tube feet facing inward. The tip of the arm was held above the animal. (3) Rolling (twisting)—an arm can be described as rolling when it twists on its axis to either side, bringing its tube feet in contact

TABLE I

Statistical analysis comparing the leading arms used in righting in Henricia leviuscula *utilizing the chi-square goodness-of-fit test*

Leading arms compared	N*	Degrees of freedom	Computed X^2 values	Probability of a larger X^2
C and A	106	1	4.56	0.050**
C and B	110	1	2.94	0.100
C and D	127	1	0.007	0.950
C and E	109	1	3.31	0.100
D and A	105	1	4.20	0.050**
D and B	109	1	2.65	0.110
D and E	108	1	3.00	0.100

* Total number of times the two arms are used as leading arms, based on 130 trials.
** Significantly different at the 5% level.

with the substratum. All possible combinations of the major righting movements, lowering, raising, and rolling of the arms, resulted in the sea star turning over.

Detailed description of righting reactions

In *H. leviuscula*, during the pre-righting period the ambulacral grooves opened wide and the tube feet were extended. Next, the tube feet on one arm all extended in one direction. As the reaction proceeded, the other four arms were lowered and eventually brought their aboral surfaces in contact with the substratum, and their tube feet pointed in the same direction as those of the arm first lowered. While the arms were being lowered, they were usually also rolling. Once the substratum had been gripped, four or five arms (one sometimes temporarily remaining inactive) began to roll to one side or the other. Eventually, two arms rolled so that their ventral surfaces faced each other. They then began "walking" to the side of the animal bringing more and more tube feet into action. These two arms are called the leading arms in this discussion. As these two arms moved to the side of the animal, one or two of the remaining arms released themselves and swung over the sea star until their ventral surfaces reached the bottom. The other arm(s) was then pulled over, so that the animal in effect turned a somersault.

L. aequalis used either the folding over or somersaulting method when righting. Occasionally, a combination of both righting methods was used. Following the pre-righting period, five or six arms were lowered, bringing their aboral surfaces in contact with the substratum. As these arms lowered they were usually rolling distally. Once the substratum had been gripped, three to six arms began rolling to either side. The lowering and rolling phases were followed by one of the three types of reactions described below.

First, two of the arms that were rolling on the substratum eventually twisted so that their ventral surfaces faced each other. Except for the fact that one additional arm swung over, the rest of the righting reaction was very similar to the righting method described for *H. leviuscula*.

Secondly, three adjacent arms that were rolling on the substratum twisted so that the ventral surfaces of the outer arms eventually faced each other. These became the leading arms. The arm between the two leading arms remained pas-

TABLE II

Statistical analysis comparing the leading arms used in righting in Leptasterias aequalis *utilizing the chi-square goodness-of-fit test*

Leading arms compared	N†	Degrees of freedom	Computed X^2 values	Probability of a larger X^2
A and B	194	1	0.08	0.900
A and C	176	1	2.75	0.100
A and D	165	1	6.66	0.010**
A and E	189	1	0.42	0.750
A and F	192	1	0.19	0.750
B and C	172	1	1.88	0.250
B and D	161	1	5.23	0.025*
B and E	185	1	0.14	0.750
B and F	188	1	0.01	0.900
C and D	143	1	0.84	0.500
C and E	167	1	1.01	0.500
C and F	170	1	1.51	0.250
D and E	156	1	3.69	0.100
D and F	159	1	4.58	0.050*
E and F	183	1	0.05	0.900

† Total number of times the two arms are used as leading arms, based on 260 trials.
* Significantly different at the 5% level.
** Significantly different at the 1% level.

sive and later doubled under the disc or walked backwards under the sea star. As the two leading arms moved to the side of the animal, one, two, or three of the remaining arms released and swung over the sea star. Finally, the other arms were pulled over until their ventral surfaces reached the substratum.

Thirdly, four adjacent arms that were rolling on the substratum eventually twisted so that the ventral surfaces of the two outer arms faced each other. The two middle arms either remained passive and later doubled under the disc or walked backwards under the animal. The two remaining unattached arms were finally pulled over by the action of the four attached arms.

In *L. aequalis,* the coordinated tube foot movements of all arms appeared later in the righting reaction than in *H. leviuscula.* In both species this unified response was the first visible sign of coordination of all arms to produce the righting movement.

Leading arms

In order to determine whether or not *H. leviuscula* and *L. aequalis* showed a preference for using a particular arm or combination of arms to turn over in the righting reaction, the data were subjected to statistical analysis by the chi-square goodness-of-fit test. The results are summarized in Tables I to IV.

For the statistical analysis each arm was first considered separately, even when functioning as a member of a pair of leading arms.

TABLE III

Statistical analysis comparing the leading pairs of arms used in righting in Henricia leviuscula *utilizing the chi-square goodness-of-fit test*

Leading pairs of arms compared	N*	Degrees of freedom	Computed X^2 values	Probability of a larger X^2
C/D and A/B	60	1	5.40	0.025**
C/D and B/C	64	1	3.08	0.100
C/D and D/E	63	1	3.57	0.100
C/D and E/A	60	1	5.40	0.025**

* Total number of times the pairs of arms were used as leading pairs of arms, based on 130 trials.
** Significantly different at the 5% level.

From the data presented in Table I it can be noted that *H. leviuscula* used arms C and D more often as leading arms than arms A, B, and E. When arms C and D were compared they were found to be used as leading arms equally. Only when arms C and D were compared with arm A were they found to be used significantly more often as leading arms.

Analysis of the data on leading arms in *L. aequalis,* indicated that in this species also, certain arms were used more as leading arms than other arms. The results are shown in Table II. Arms A, B, E and F were used more as leading arms in the righting reaction than arms C and D. Also, the data showed that arms A, B, E and F were all used equally as leading arms, as were arms C, and D. Only when arms A, B, and F were compared to arm D were they found to be used significantly more often as leading arms.

It was previously shown that, when righting, both species preferred the variation of the somersaulting method using two adjacent arms. The next step in the analysis was to determine whether or not either species showed preference for any pair of adjacent arms. In 15% of the 260 trials, *L. aequalis* used three or four arms as a leading group when using the folding over method. These data were not used in the analysis of pair preference.

In *H. leviuscula* the combination of arms C/D was used more as a leading pair of arms than the pairs A/B, B/C, D/E, and E/A (Table III). Only when the pair of arms C/D was compared with the combination of arms A/B, and E/A, was it found to be used significantly more often as a leading pair of arms.

Analysis of the data on leading pairs of arms in *L. aequalis* indicated that the pair or combination of adjacent arms A/B, B/C, E/F, and F/A were used more often as leading arms in the righting reaction than arms C/D and D/E (Table IV). The pair of arms C/D and D/E were used equally as often as leading arms in the righting reaction, as were the pairs A/B, B/C, E/F and F/A. Only when the pairs of adjacent arms A/B, B/C, and E/F were compared to C/D were they found to be used significantly more as a leading pair of arms.

Time

The time required for righting in *H. leviuscula* was very variable, ranging from 94 to 570 seconds. The average time taken was 230 seconds. In *L. aequalis,* variability in righting time ranged from 67 to 664 seconds for the somersaulting

TABLE IV

Statistical analysis comparing the leading pairs of arms in righting in Leptasterias aequalis *utilizing the chi-square goodness-of-fit test*

Leading pairs of arms compared	N*	Degrees of freedom	Computed X^2 values	Probability of a larger X^2
A/B and B/C	88	1	0.00	0.000
A/B and C/D	66	1	7.30	0.010**
A/B and D/E	74	1	2.64	0.250
A/B and E/F	87	1	0.00	0.900
A/B and F/A	81	1	0.60	0.500
B/C and C/D	66	1	7.30	0.010**
B/C and D/E	74	1	2.64	0.250
B/C and E/F	87	1	0.01	0.900
B/C and F/A	81	1	0.60	0.500
C/D and D/E	52	1	1.23	0.500
C/D and E/F	65	1	6.80	0.010**
C/D and F/A	59	1	3.81	0.100
D/E and E/F	52	1	2.26	0.250
D/E and F/A	67	1	0.70	0.500
E/F and F/A	80	1	0.45	0.500

* Total number of times the pair of arms were used as leading pairs of arms, based on 220 trials.
** Significantly different at the 1% level.

method and from 100 to 623 seconds for the folding over method. The average time taken was 168 seconds for the somersaulting method and 195 seconds for folding over. Analysis of the data showed that there was no significant difference in righting time between the somersaulting and folding over method in *L. aequalis* ($X^2 = 2.01$; d.f. = 1; $P = 0.20$).

Time-size relationship

In order to determine whether there was a significant relationship between body size (the R measurement) and the righting time in *H. leviuscula* and *L. aequalis,* the variance, standard deviation, and standard errors of the righting time was determined for each of the three size categories for both species (Tables V and VI). Righting time ranged from as much as 400 seconds in large individuals to 200 seconds in smaller individuals.

For each species the mean righting times of the three size classes were compared using the t-test. In *H. leviuscula* (Table VII) a significant difference was found between the righting times of small and medium sized individuals ($t = 2.79$; d.f. = 26; $P = 0.005$), and medium and large sized individuals ($t = 6.64$; d.f. = 26; $P = 0.005$). In *L. aequalis,* when small and medium sized individuals were compared, it was found that there was a significant difference between their righting times ($t = 4.39$; d.f. = 26; $P = 0.005$). The same was true of medium and large sized individuals ($t = 1.71$; d.f. = 26; $P = 0.10$). These facts suggest that

TABLE V

Summary of statistical analysis of the righting times in Henricia leviuscula *of different sizes*

Trial	Sum (Seconds)	$\bar{y}$	Range	S^2	s	S.E.	N*
Small (R = 0.4–2.8 cm)							
A	1019	113	81–168	806	28	9.46	9
B	1378	153	86–230	3,145	56	18.70	9
C	1394	155	127–196	796	28	9.40	9
Total	3791	140	81–230	1,849	43	8.26	27
Medium (R = 3.1–4.8 cm)							
A	1766	177	100–412	7,951	89	27.90	10
B	1823	182	84–323	7,809	88	27.63	10
C	2014	201	128–307	3,985	63	19.72	10
Total	5603	187	84–412	6,244	79	14.36	30
Large (R = 5.0–10.1 cm)							
A	2776	308	165–426	9,877	99	33.10	9
B	3283	365	233–524	12,895	114	38.00	9
C	3421	380	274–554	9,509	98	32.66	9
Total	9480	351	165–554	10,918	105	20.99	27

* Total number of times animals were turned over

there was a significant relationship between the body size and the righting time in both species of sea stars, with smaller individuals righting faster than larger.

It was also observed that *H. leviuscula* took longer times to right in successive trials, even with six and 12 hour rest intervals between trials (Table V). This was not true of *L. aequalis* (Table VI).

Mechanical stimulation

Sea stars were turned over by picking them up by the tip of one arm. The possible effect on the frequency of the use of such arms as lead arms was studied by analyzing the data with the chi-square goodness-of-fit test.

Regardless of which arm was used to turn *H. leviuscula* over, the arm so stimulated was used with the same frequency as a leading arm as each of the other arms. Therefore, in *H. leviuscula* mechanical stimulation did not affect the use of an arm as a leading arm in any way.

On the other hand, analysis of the effects of mechanical stimulation on *L. aequalis* indicated that regardless of which arm was used to turn the sea star over, the arm so stimulated was used less as a leading arm than each of the other arms.

Further statistical analysis on the effect of mechanical stimulation showed that in most instances the arm used to turn the sea star over was used less as a leading arm than it would have been if that arm had not been used to turn the sea star over and less than each of the other arms.

TABLE VI

Summary of statistical analysis of the righting times in Leptasterias aequalis *of various sizes*

Trial	Sum (Seconds)	$\bar{y}$	Range	S^2	s	S.E.	N*
Small (R = 0.8–1.9 cm)							
A	1160	145	86–236	3,441	59	20.85	8
B	1604	160	95–379	7,211	85	26.87	10
C	1223	136	83–269	3,263	57	19.03	9
Total	3987	148	83–379	4,536	67	12.45	27
Medium (R = 2.1–2.9 cm)							
A	3028	303	123–576	14,767	122	38.40	10
B	2127	213	157–407	5,030	71	22.44	10
C	2332	233	156–484	9,837	99	31.39	10
Total	7487	250	123–576	10,735	104	18.92	30
Large (R = 3.0–4.1 cm)							
A	3127	347	199–737	29,374	171	57.13	9
B	2285	254	151–585	24,161	156	51.83	9
C	2970	330	183–694	30,537	175	58.23	9
Total	8479	310	151–737	35,494	188	36.26	27

* Total number of times animals were turned over

DISCUSSION

Variation in the righting method has been attributed to many extrinsic and intrinsic factors (Reese, 1966). In this work, the methods of study and maintenance of laboratory animals were designed so that as many of these factors as possible were kept constant, or variation in them kept minimal.

Somersaulting characterized the righting method employed by both *H. leviuscula* and *L. aequalis.* In contrast, the folding over method, and a combination of folding over followed by somersaulting were used only by *L. aequalis.* Table VIII summarizes the various righting methods known to be used by asteroids, and demonstrates that the method used by *H. leviuscula* and *L. aequalis* is the predominate method known.

Since representatives of all major extant orders are included, the somersaulting method described in detail here appears to be characteristic of the entire Class Asteroidea.

Evidence for the existence of a quiescent period in righting in asteroids is given by Moore (1939), Ohshima (1940), Hyman (1955), and Reese (1966). The present study indicates that *H. leviuscula* and *L. aequalis* are active during the pre-righting period, suggesting that there is no true quiescent period in these species. Evidence was found by the author that *Astropecten brasiliensis armatus* and *Patiria miniata* (Polls, unpublished data) also have no quiescent period.

TABLE VII

Statistical analysis comparing the righting times of various size categories of Henricia leviuscula *and* Leptasterias aequalis *utilizing the t-test*

Species	Size categories compared	N†	Degrees of freedom	Computed t value	Probability of a larger t
Henricia leviuscula	Small and Medium	57	26	2.79	0.005**
	Medium and Large	57	26	6.64	0.005**
Leptasterias aequalis	Small and Medium	57	26	4.39	0.005**
	Medium and Large	57	26	1.71	0.050*

† Total number of times animals were turned over.
* Significantly different at the 5% level.
** Significantly different at the 1% level.

Due to the shortness of the pre-righting period, no attempt was made to discover which arms were actually moving first, nor how this might affect the role played by these individual arms during the rest of the righting reaction. Additional observations are needed to answer questions on the specific order and nature of the pre-righting motions, and their significance.

During the pre-righting period, the sea star may be sensing its inverted position and relaying this sensory information by way of the nervous system to other parts of the body. Apparently, once the inverted orientation has been detected and nervous integration accomplished, the righting reaction can be initiated.

Following the pre-righting period, the tube feet of all the arms are extended outward in many directions. Once the initial, oriented, tube feet movements appear, all activities of the sea star are committed towards turning in a certain unified way and direction. The establishment of righting response implies a coordinated activity of all the arms and the tube feet.

Coordinated arm movements were clearly present in *H. leviuscula* at the beginning of the righting reaction but, in *L. aequalis*, they appeared later. Early coordinated movements have also been observed in other asteroids by Jennings (1907), Cole (1913b), Kjerschow-Agersborg (1918), Russell (1919), Hamilton (1922b), and Moore (1939).

Jennings (1907) lists a number of factors which may determine the direction of the righting movements, the most important of which is the tendency to right with a fixed pair of arms. Once the tube feet of these arms are all extended in the same direction, these arms become the leading arms. In other words, once the righting response appears, one can tell early in the righting reaction which will be the leading pair of arms.

The results of this study show that following the righting response, the attached tube feet of the non-leading arms let go (releasing response) and extend in the direction of the leading arms.

Hamilton (1922b), Moore (1945), Kerkut (1954), and Smith (1965) also found that following the righting response the tube feet of the subordinate arms detach. Suppression of activity by the tube feet of non-leading arms thus plays a critical part in the first movements of the righting reaction. No causal explana-

TABLE VIII

Righting methods used by asteroids

Order	Species	Most Common Righting Methods	Investigator
Phanerozonia	*Astropecten auranciacus*	Somersaulting and tulip	Romanes (1885)
	Astropecten brasiliensis armatus	Tulip	Polls (unpublished)
	Oreaster nodosus	Folding over	Ohshima (1940)
Spinulosa	*Asterina gibbosa*	Somersaulting and folding over	Russell (1919)
	Henricia leviuscula	Somersaulting	Polls (1969)
	Patiria miniata	Somersaulting	Polls (unpublished)
	Pteraster tesselatus	Somersaulting	Rodenhouse and Guberlet (1946)
Forcipulata	*Asterias forbesi*	Folding over	Cole (1913a, 1913b)
	Asterias rubens	Somersaulting	Romanes and Ewart (1881) Romanes (1885) Smith (1950)
	Astrometis sertulifera	Somersaulting and folding over	Jennings (1907)
	Leptasterias aequalis	Somersaulting	Polls (1969)
	Pisaster ochraceous	Somersaulting	Moore (1910a, 1910b) Hamilton (1921, 1922a, 1922b)
	Pycnopodia helianthoides	Combination of somersaulting and folding over	Kjerschow-Agersborg (1918)

tion for this suppression, which must require central nervous system integration, can be given at this time.

Many investigators have attempted to discover whether there is a physiological anterior end involved in righting. The literature dealing with this question falls into two major categories. Ohshima (1940) found no dominant or leading arms in righting, and consequently no anterior end. In contrast, Jennings (1907), Cole (1910, 1913a, 1913b), Cowles (1910, 1911), Kjerschow-Agersborg (1918, 1922), Russell (1919), Hamilton (1922a), Rodenhouse and Guberlet (1946), Smith (1950), and Polls (unpublished data) reported that there is a physiological anterior end marked by a dominant pair of arms.

Since the results of this study show that there was a leading pair of arms in both *H. leviuscula* and *L. aequalis* they support the idea that sea stars have a physiological anterior end. It is not known why sea stars use one combination of arms more frequently than others as a leading pair, nor why different species use different pairs.

Reese (1966, page 179), after reviewing the literature on righting in Echinoderms, concludes that "there is a tendency for one pair of arms—usually at least one arm of the pair is adjacent to the madreporite—to lead the righting movement." However, he further says that this preference for one pair of arms is an individual rather than a species characteristic.

In this study it was not possible to follow the behavior of individuals since various marking techniques such as vital dyes and tagging were unsuccessful. Although some sea stars may exhibit individual preference for a leading arm, the results of this study show that in *H. leviuscula* and *L. aequalis* the preference for certain arms to lead in the righting reaction is a species rather than an individual characteristic.

While *H. leviuscula* and *L. aequalis* showed a preference for certain arms to lead in the righting reaction, these are not adjacent to the madreporite. The position of the madreporite may have indirect significance in arm preference during righting in asteroids. Unfortunately, there is no information in the literature on how the madreporite is related to the central nervous system, nor is there any obvious asymmetry of the nervous system in the madreporite region. The madreporite remains a curious bench-mark.

It was observed that in *H. leviuscula* and *L. aequalis*, the preference for a specific arm is not due to the length of the arm, or greater number of tube feet as suggested by Hamilton (1922a), since the leading arms were the same length as the non-leading arms. This also was found by Cole (1913a) in *Asterias forbesi*, Crozier (1920) in *Coscinasterias tenuispina*, and Smith (1950) in his study of *Asterias rubens*.

The time required to right from mechanical inversion to the natural posture varied considerably in both *H. leviuscula* and *L. aequalis*. Variability in the righting time has also been reported by Cole (1913b), Ohshima (1940), and Rodenhouse and Guberlet (1946).

Kleitman (1941) found that there was a relationship between righting time and temperature, with righting time increasing as the temperature rose. The temperature was not controlled during the trials in this study. The possible effect of the approximately 5° C temperature variation between experiments was not analyzed. Analysis of the data shows a strong relationship between size and time. Any possible effects of temperature were probably less than the effect of size on time of righting.

Asterias, Asterina, Leptasteria, and *Pycnopodia* have soft, flexible bodies, slender arms (except *Asterina*), and strong tube feet. The species studied in these genera can right quite rapidly. Cole (1913b) reported that the average time for *Asterias forbesi* was 160 seconds. Russell (1919) found it to be 30 to 45 seconds for *Asterina gibbosa*. For *L. aequalis*, the average time was 181 seconds. Kjerschow-Agersborg (1918) reported that the average time for *Pycnopodia helianthoides* to be 57.1 seconds.

In contrast, *Henricia* and *Oreaster* have stiff, non-flexible bodies, the tube feet are weak, and they take much longer to right than other species. The average time taken to right for *H. leviuscula* was 230 seconds. Ohshima (1940) discovered it to be 360 to 420 seconds for *Oreaster nodosus*. Differences in righting time between species appear to be primarily an expression of differences in morphology rather than of environmental variables or behavioral modes.

The great variation observed in the righting time in both species studied raised the question of the possible relationship between the size of the sea stars and their righting times. The statistical analysis showed that there was a significant relationship between body size and righting time ($P = 0.005$) for both species. This suggests that with an increase in body size there is an increase in the length of time taken to right within a species of asteroid.

Therefore, since a relationship has been shown between righting time and body size, it is probable the average righting times given for other species of asteroids may have been influenced by the size of the sea stars used. Unfortunately, no size categories were given for the sea stars used in previous time-study investigations.

It was also observed that after six or even 12 hour rest intervals before being turned over again, *H. leviuscula* took a longer time to right. The same phenomenon was not observed in *L. aequalis.* Kjerschow-Agersborg (1918) and Ohshima (1940) found after repeated trials, the righting time increased, which they interpreted as fatigue. Jennings (1907) noted that after repeated turning over of the same individual, there was no improvement in the time taken to right.

It is possible that the increase in righting time observed in *H. leviuscula, Pycnopodia helianthoides,* and *Oreaster nodosus,* may be due to a process similar to habituation.

The statistical analysis demonstrated that in *L. aequalis,* the arm used to turn the sea star over was used less frequently as a leading arm. No such effects of mechanical stimulation on a leading arm were observed in *H. leviuscula.*

This evidence supports the suggestions of Jennings (1907) and Smith (1950) that an arm used most frequently as a leading arm is conditioned by imposed external stimulation. Smith (1950) also states that intensive stimulation of leading arms causes that arm to be used less as a leading arm. Similar observations have been noted by Polls (unpublished data) in *Patiria miniata.*

These findings suggest that if previous investigators turned over the sea stars by the same arm on each trial, then perhaps the leading arms they found were not the true leading arms. In many reports on righting in asteroids, no mention is made as to which arm(s) was used to turn the sea stars over.

H. leviuscula and *L. aequalis* live on intertidal rocky shore areas which are exposed to heavy wave action. Therefore, a righting reaction in this habitat is of obvious survival advantage.

The statistical analysis demonstrated that there was no difference in the righting time between the somersaulting and folding over method in *L. aequalis.* Therefore, neither method would appear to be more advantageous for survival in nature. Field studies on the frequency and circumstances of use of the two methods may reveal their significance.

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Summary

1. The behavioral aspects of righting were studied in the asteroids *Henricia leviuscula* and *Leptasterias aequalis* by detailed observations on the righting method, including leading pair of arms and righting time.

2. Somersaulting characterized the righting method employed by both species. In contrast, the folding over method, and a combination of folding over followed

by somersaulting were used only by *L. aequalis*. Somersaulting appears to be characteristic of the entire class Asteroidea.

3. Both species are active during the pre-righting period, suggesting that there is no entirely motionless quiescent period.

4. The righting response was clearly present in *H. leviuscula* at the beginning of the righting reaction. However, in *L. aequalis,* it appeared later.

5. *H. leviuscula* exhibited a tendency to utilize arms C/D more as the leading pair of arms than other arm pairs. In *L. aequalis*, arm pairs A/B, B/C, E/F, and F/A were used more as leading arms than arm pairs C/D and D/E. In both species the preference for certain arms to lead in righting reaction is a species rather than an individual characteristic. Leading arms are not adjacent to the madreporite.

6. The time required for righting in both species was very variable. Differences in righting time between species appears to be an expression of differences in morphology rather than of environmental variables or behavioral modes.

7. There was a significant relationship between the body size and the righting time in both species of sea stars, with smaller individuals righting faster than larger.

8. Mechanical stimulation affected the arms used in righting in *L. aequalis*. The arm used to turn the sea star over was used less frequently as a leading arm. It is possible that the results of some previous studies are in error because of this response. However, no such effects were observed in *H. leviuscula*.

9. Since there was no difference in the righting time between the somersaulting and folding over method in *L. aequalis*, neither method would appear to be more advantageous for survival in nature.

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